

Seasonal and reproductional polymorphism in *Ceratophysella sigillata* (Uzel) (Collembola, Hypogastruridae)

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Two new polymorphisms were observed in *Ceratophysella sigillata*: an inactive summer dormancy and an epitoky in spring. During a single year, the species passes through four different morphs: A (active), B (active, transition to C), C (inactive) and E (epitoky). C and E cannot be determined with actual keys, and show characteristics similar to those of other epitokic *Ceratophysella*. The features checked in our study were: mucro, setae on dens, tibiotarsal spur hair, protrusile antennal vesicle. As the life span of an individual may extend beyond two years, it passes through both polymorphisms more than once. *C. sigillata* is the only collembolan known with two polymorphisms combined.

1. Introduction

In Hypogastrurids, three types of polymorphism are known:

1. *Epitoky* is linked with the reproductive cycle. It was investigated in detail by Cassagnau and his team (e.g. Bourgeois & Cassagnau 1970, Bourgeois & Cassagnau 1973, Bourgeois 1974) and reported mainly for *Ceratophysella* species.
2. *Ecomorphosis* is induced by environmental factors, but genetic factors may also be involved. It includes a number of physiological adaptations to an adverse summer climate. Detailed studies were carried out on *Hypogastrura purpureascens* and *H. boldorii*, again by the team of Cassagnau (e.g. Cassagnau 1955, Bedos 1986, Cassagnau 1986, Bedos & Cassagnau 1988).
3. *Cyclomorphosis* is another seasonal polymorphism, known in *Hypogastrura socialis* and *H. lapponica* (Leinaas 1981a, b), which are active on the surface in winter. The winter morph is considered as an adaptation to an adverse winter climate.

The biology of *C. sigillata* was largely unknown until now, only some mass occurrences during winter having been mentioned in the literature (for details see Zettel & Zettel 1994). This paper reports the results of the first two years of our research project.

2. Material and methods

The population investigated is located in a mixed forest 10 km north of Berne, Switzerland, at an altitude of 640 m a.s.l.

Population samples were collected at regular intervals on the surface and in the soil. Most measurements and determinations were made on freshly caught animals. A number of cultures were kept in climatic chambers with a simulated natural light and temperature regime and fed with a mixture of yeast, *Pleurococcus* algae and ground oats. The culture jars consisted of 60 and 400 ml glass vials with a bottom layer of moistened plaster of Paris mixed with charcoal, and a tight lid. In order to prevent the formation of condensed water, and the animals from escaping through tiny gaps between lid and glass, we placed a thin cardboard disc inside the lid.

The instars were identified primarily by their mucro shape and size, which proved to be much more reliable than total body length (for details see Zettel & Zettel 1994). We also checked the dens with medio-distal setae, tibiotarsal spur hair, and protrusile antennal vesicle. The development of cultured animals did not differ from that at the field site.

3. Results

3.1. Development and succession of morphs

Ceratophysella sigillata grows to a total body length of about 1.2 mm. During their development, the individuals pass through four different morphs which we call A (active), B (active, transition to C; in sensu Cassagnau), C (inactive, summer dormancy) and E (epitoky). A and B correspond to the known taxonomic descriptions of *C. sigillata*. C and E are very different from A and B and cannot be correctly determined with existing keys.

The succession of the different morphs during ontogeny shows a striking regularity (Table 1): two active instars are always followed by a morph which is not surface-active in the sequence A–E–B–C. The only deviation occurs at the beginning of development, the two first instars being A and followed by C.

At the end of their first year of life, during moult I_6 to I_7 , a high mortality can be observed: $47.6 \pm 11\%$ (mean $\pm 95\%$ CI), compared e.g. to that of I_5 to I_6 : $4.2 \pm 2.5\%$. The survivors live for another year, again going through all morphs. At the end of their second year, the mortality increases drastically ($88 \pm 13\%$). In our cultures, the very few animals surviving this moult in the spring of 1992 entered the C-morph phase for a third time. Because they can no longer be distinguished by their size or colouring in the field, we are not yet able to say if they may accomplish a third year of life. First and second year animals can be distinguished also in the field by their colouring; in the colonies monitored during winter up to 30% of the individuals were older than one year.

3.2. Morphs A and B

These morphs correspond to the known taxonomic descriptions of *Ceratophysella sigillata*.

Common characteristics

Morphology: The mucro is large, boat shaped, heavily sclerotized, with a prominent lateral tooth. Its length is half that of the dens. The medio-distal setae of the dens are thickened in their basal third and clearly bent. The longest (distal) spur hair on the tibiotarsus is clavate. The antennae show a protrusile vesicle between segments 3 and 4. — **Behaviour:** The animals are surface-active whenever the humidity is sufficient. In winter as well they feed on the surface or, when precipitation permits it, even on tree trunks several metres above the ground. Under certain conditions, which have not yet been analyzed, the colonies which comprise hundreds of thousands or millions of individuals start to move over the surface, with a speed of up to 30–50 cm per hour, or form aggregations several centimetres thick. During surface activity, they show a remarkable jumping behaviour, resulting in a rustling noise which can be heard at a distance of several metres.

Separating characteristics

Morphology: In morph A, mucro and body length increase with each ecdysis; in B-animals, these measurements de-

crease and the mucro is generally smaller than in A-instars of the same year. With this feature, they represent a transition to the next morph, C. — **Behaviour:** In B-animals, the surface activity is less prominent than in A-animals.

3.3. Morphs C and E

Common characteristics

Morphology: The expression of the features exhibits a broader variability than in morphs A and B. The mucro is half the size of that in the other morphs, the ratio dens:mucro being 4:1. It is more delicate, only slightly boat-shaped, and a small lateral tooth may be present or absent. The two medio-distal setae of the dens are more slender, of the same diameter as the next setae; they are not bent, but only slightly curved. The antennae lack a protrusile vesicle. The tibiotarsal spur hair is pointed. — **Behaviour:** usually both morphs do not feed, but their gut is not atrophied. They are never visible on the surface and remain in the F-layer during the whole instar.

Separating characteristics

Morphology: Sex determination is only possible in morph E (and the last days of the preceding A-instar). Differentiation is not only possible using the genitalia: females have an inflated abdomen and a speckled grey-brown colouring, while males have a normal shape and are darker and not speckled. The E-morph lasts about three weeks in April/May. The C-morph, as a dormant instar, lasts 4–5 months, from May/June to the end of October. Second year animals enter the C-morph phase earlier than first year animals do. — **Behaviour:** E-instars are quite active, crawling about, but not readily jumping. By contrast, C-animals form dense clusters in the F-layer (or in the culture jars), remaining motionless for months (being in body contact and the antennae bent downwards, they have a striking resemblance to a flock of sheep). Finally, reproduction only occurs in the E-morph.

4. Discussion

The epitoky of *Ceratophysella sigillata* fits the descriptions of that of other *Ceratophysella* species investigated by Bourgeois: *C. acuminata*, *armata*, *denticulata*, *tuberculata* and *norensis* (e.g. Bourgeois 1973, 1974). The morphological similarity of morphs E and C is striking, which may be the reason why morph E was first called B (=C) by Bour-

Table 1. Succession of morphs during ontogeny of *Ceratophysella sigillata*.

	1st year						2nd year						3rd year		
Month	M	J	J	N	F	M	A	A	M	N	F	M	A	A	M
Instar	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Morph	A	A	C	A	A	E	B	B	C	A	A	E	B	B	C ?

geois & Cassagnau (1970). These authors already supposed some relationship between epitoky and ecomorphosis (Bourgeois & Cassagnau 1973). Looking at our observations, a very close relationship between these two polymorphisms is obvious, as they occur in the same species and in a regular pattern.

We still hesitate to call the summer dormancy of *Ceratophysella sigillata* an ecomorphosis as long as the actual triggers are unknown. In the cases of *Hypogastrura boldorii* and *H. purpureascens* investigated by the team of Cassagnau the influence of high temperature for the induction of the change of morph could be demonstrated (Cassagnau 1955, 1986, Bedos 1986, Bedos & Cassagnau 1988). We already have some evidence that temperature may play a role, but further experiments are necessary. In cultures, *H. boldorii* changed to the C-morph when temperatures rose to 25°C. Ecomorphosis is considered to be an adaptation to the warm and dry summer climate in the mediterranean region. As *C. sigillata* lives in forests, surface temperatures never rise to such temperatures regularly and noon peak temperatures rarely exceed 20°C. When the instars changed to the C-morph, mean surface temperatures were only 10–15°C, which are almost the same values as in April, before the budding of the beech. Therefore, high temperatures do not seem to necessarily initiate ecomorphosis in this climate. North of the alps, there is only one record of an ecomorphosis (*H. purpureascens* in Geneva; Gisin 1949). Experiments and measurements are under way to elucidate triggering in *C. sigillata*.

Bedos (1986) and Bedos & Cassagnau (1986) demonstrated that beside the effect of environmental factors an endogenous triggering may be involved as well in some populations of *Hypogastrura boldorii*.

As well as the morphological similarity of the C-morph in *Ceratophysella sigillata* and *Hypogastrura boldorii* there are some distinct differences. In *H. boldorii* the gut is atrophied and no longer functional, whilst in *C. sigillata* the digestive tract is not reduced. At the beginning of the C-instar, we found a good percentage of animals with gut content.

Bedos (1986) mentions that the body length is reduced by 50% in C-animals of *Hypogastrura boldorii*. In *Ceratophysella sigillata* the summer morph is also smaller than the preceding instars, but the difference is about 5%.

Morph B seems to be much closer to A in *Ceratophysella sigillata*. In *Hypogastrura boldorii* it is, also according to its behaviour, rather closely related to C.

There is no relationship between the polymorphisms observed in *Ceratophysella sigillata* and those in the three other winter-active Collembolans investigated so far. *Hypogastrura socialis* and *H. lapponica* show a seasonal dimorphism (Leinaas 1981a, b), termed cyclomorphosis by Fjellberg (1986), with a distinct single instar in the winter morph. The same was observed in *Isotoma hiemalis*, in which the trigger is an endogenous circannual rhythm (Zettel 1985) being synchronized with the seasons by use of the photoperiod (Zettel & Zettel 1989). In *C. sigillata* there is no special winter instar; the sequence of two A-morphs is a distinct feeding phase in contrast to the starving surface active animals of *H. socialis* and *I. hiemalis*.

So far, *Ceratophysella sigillata* is the only Collembolan known in which two polymorphisms are combined.

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